THE PHYSIOLOGICAL WATER REQUIREMENT AND THE GROWTH OF PLANTS IN GLYCOCOLL SOLUTIONS[1]

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The relation of plants to peat and humus soils has been of the utmost importance to students of plant physiology because of the nature of the metabolism involved. It is of equally great interest to ecologists in so far as the native social vegetation units covering an organic soil area take on a characteristic spacial distribution—a mutual exclusiveness—and yet gradually intrude upon and replace one another in a fairly genetically related succession in time.

The contributions of the senior author (5–8) have been mainly with a view toward an analysis of the several habitat factors, and a study of the organic constituents of peat soils in relation to plant activity. Historical accounts and a number of experimental data on the causal and limiting factors of a bacterial, chemical, and other nature have been brought together in Bulletin 16, Geological Survey of Ohio, 1912 (7).

The present paper, though only of a preliminary nature, is a continuation of the physiological studies and has been made in the hope that it will draw more pointed attention to the metabolic processes of a number of plants, some of which do, while others do not, seem to be able to extend their range of distribution beyond a typical habitat. In addition, the attempt is made with a view to understanding more clearly the nature of the "association factor" which seems of great importance in determining the geographical distribution of the higher social vegetation units, and the edaphic "preferences" of plants more or less nomadic in their tendency.[2]

The principal organic compounds from which peat and humus are derived are the various lignocelluloses, the carbohydrates, proteins

[1] Contribution from the Botanical Laboratory of Ohio State University, No. 82.

[2] A more explicit statement will appear shortly dealing with the association factor and the evolution of social vegetation types, based upon observations which one of the authors obtained during the recent International Phytogeographic Excursion in America.

and other substances produced in the course of the growth and reproduction of bog and swamp vegetation. During the decomposition of these by weathering and biochemical changes, by bacteria and fungi, various other compounds and transition products arise. The definite recognition of a number of these constituents from mineral soils has led to a fuller understanding of the chemistry of organic soils (16), but for many of the peat and humus compounds the names and written reactions have little meaning as now understood; the organic degradation products are of great complexity and they cannot as yet be easily isolated and identified. It is well known, however, that during a gradual hydrolysis of proteins, for example, there arise chiefly diamino and monoamino acids. Glycocoll, $H_2C.NH_2.COOH$, is one of the simpler degradation products and has been derived from the tissue and the seeds of a number of plants.

Important problems of agriculture and economic considerations are involved in the ability to accomplish the growth of crop-yielding plants within a shortened life cycle and at lessened energy requirements and expense. Hence the question of the efficiency of a plant in utilizing directly nitrogenous compounds other than nitrates and ammonia has interested a number of investigators, both from the standpoint of the problems of soil fertility and that of plant metabolism and enzyme action. Hansteen (11), Molliard (13), Schreiner (15), Hutchison and Miller (12), and Borowikow (1) have ascertained the effects of water solutions of glycocoll on plants. They report, more or less uniformly, that the effects of glycocoll are beneficial, and that a gain results of nitrogenous matter in the plants. Hansteen found that *Lemna* in the absence of light produces proteins, but that the effect on growth is slightly harmful. Molliard obtained better results with radishes. Schreiner found that glycocoll is beneficial to wheat seedlings in solutions containing 0.1 per cent and less of the solute. Hutchison and Miller working with peas report inconclusive results; the nitrogen content of one of the pea-cultures was increased, but a slight decrease was noticed in another culture. The more recent experiments of Borowikow with *Helianthus* indicate that the solution retards growth.

It is not known to what extent amino-acids occur in peat soils. Although we are unable to extract at present any beneficial nutritive materials from them by ordinary chemical means, it is quite likely that many of the bacteria and fungi are able to do so by excreting enzymes with dissolving capacities. The question possesses additional

interest in the case of heaths and other bog plants having mycorrhiza, since we have no knowledge of the form of organic peat constituents which they can assimilate.

In the continuation of this work the same general methods described in previous publications have been used. For the glycocoll employed in these experiments we are indebted to Prof. W. McPherson, of the department of chemistry of this University, whose interest in this problem has been voiced in his vice-presidential address before section C of the American Association for the Advancement of Science (10). Grammolecular solutions of varying concentrations were prepared in distilled water which had been filtered through carbon (lamp black). The experiments were begun in October, 1913. The bog plants used in these tests were obtained, in November, 1913, from the cranberry-sphagnum association on Cranberry Island at Buckeye Lake, Ohio.[3] With the exception of wheat, these and all other plants used were cuttings of known green weight. The plants were freed from dead material, washed repeatedly in distilled water, fastened to sterilized perforated corks by means of absorbent cotton, and transferred to sterilized, wide-mouthed, paper-covered glass jars of 500 cc. capacity. No other precautions were taken against the presence of nitrifying or other organisms. Although sterilization was imperfectly maintained, the results obtained with the selected series are fairly satisfactory. Each experiment was continued for 7 to 14 days, according to the amount of water transpired before renewing the culture solution. The different cultures always stood side by side in the university greenhouse. A record was kept of the weight of water absorbed and the quantity transpired. The difference between the initial and final green weight of the plants was taken to represent the amount of growth.

The original intention, to show what quantities of glycocoll are assimilated directly and thus increase the dry weight of plants, could not be adhered to in this series of experiments. Arrangements have been completed whereby the biochemical investigations of the problem will be carried out as soon as the improvements in the equipment of the new laboratory devoted to this work have been provided. For the present only a few of the preliminary experiments are here grouped according to the response of the plants and indicated by data on transpiration, amount of water absorbed and retained, and the gain or loss in the weight of plants. Related data from experiments with cuttings

[3] Geol. Sur. Ohio Bull. 16: 239.

of tomato, Eupatorium sp., and various cereals in nutrient solutions are omitted; also the results with plants cultivated under humid and arid atmospheric conditions, and, with such, the growth and stem elongation of which terminates with the formation of flowers and seeds. In the main the data correspond with the conclusions drawn from the experiments submitted in Tables I to IX, and show that transpiration is not directly correlated with and hence not a measure of growth.

The chief results of the experiments given below may be described as follows: The plants grown in the glycocoll solutions show an increase in green weight above that of the quantity of water absorbed from the solution and retained within the tissues. The predominant constituent of this gain is in part undoubtedly the glycocoll absorbed and assimilated, and to a lesser degree due to the photosynthesis of carbohydrates.

To what extent irregularities of growth tend to be followed by compensatory processes is not known. The loss in weight of plants indicated in Tables I and VII does not express a more or less prolonged rate of transpiration in excess of the rate of absorption for the same period. No loss of turgor and no form of wilting, temporary or permanent, is here involved (2, 4, 9). The deficit is in the removal of reserve materials from the tissues, and is unaffected by the external set of atmospheric conditions under which the plants were transpiring. The apparently inevitable conclusion is entertained that the problem of the water requirement of plants and the criteria for the wilting coefficient, in particular the relation between the water content of the plant and that of the soil at the time of wilting, need to be investigated more quantitatively than has been heretofore attempted. Investigations are now in progress.

The plants in solutions 2, 3, 4 (Table IV), 5 (Table V), and 3 (Table VII), retained their weight but changes were going on in the body proportions of roots. It is obvious that the constancy of the green weight of plants is therefore not an indication of lack of growth, *i. e.*, growth increments are not the only criterion or the only measure of growth. No estimate can be offered as yet of the correlation between weight and size of plant under these conditions. The suppression of growth is not primarily attributable to energy requirements, as is seen in Table VII. The failure to promote growth may be due to the lack of variety and of a more balanced condition of materials for development, *i. e.*, it may be due to the inefficiency of isolated food constituents, such as glycocoll, to supply material for tissue construc-

tion. The retention of water is smaller in plants having very low food reserves, and becomes steadily less as the glycocoll content of the solution becomes decreased or the time element in the renewal of the culture solution is extended. The progressive decline in weight is obviously a pathological manifestation. Experiments are now in progress to determine also to what extent the age of plants, their resting period, and the upper and lower limit of transpiration, which plants of any species rarely exceed, may modify the percentage of water retained. Many problems regarding the absorption of CO_2 under these conditions are still in need of future investigation, especially since the importance of the atmospheric CO_2 gradient gains an unsuspected prominence in the supposition that xeromorphy of ancient and modern vegetation may be due in part to a modified gas interchange.[4]

To what extent the numerical relation between the quantity of water retained and the amount of growth provides a value which may serve as a criterion for life zones, yields of crops, and related problems of physiology and ecology remains to be determined. The present paper is intended to throw some light on the more fundamental problem of the "water requirement" (3) of plants during growth and metabolism. By way of comparison the essential data of investigations on the acid tolerance of these plants have been given in tabular form, to enable the reader to draw further conclusions on the acidity problem of peat soils.

No special discussion is required to consider the results, here presented, in detail. An examination and comparison of the data will lead to the following conclusions:

1. The value of the transpirational water loss in the experiments cited is a function of the vapor pressure of water affected by the quantity of the salts in solution, and the factors modifying the atmospheric conditions.

2. The transpiration value of plants, when correlated with physical conditions of soil solution and atmosphere influencing it, and when expressed as a ratio in terms of these or any other factor affecting it directly, should be called the *ecological* water requirement. As such it is sufficiently distinctive to characterize diverse plants and diverse habitats, and to indicate the limiting conditions and the range of deviation of the water relation of vegetation.

[4] Geol. Sur. Ohio Bull. 16: 277.

3. The process of absorption of glycocoll is not connected with the transpirational water loss, but with the differential permeability of the absorbing root cells, with the efficiency of the nutritive metabolism characteristic of the plant and the amount of water retained within the plants.

TABLE I

TRANSPIRATION AND GROWTH OF *Scheuchzeria palustris* IN GLYCOCOLL SOLUTIONS
December 17, 1913, to January 17, 1914

Culture Solution	Amount of water in grams			Gain or loss in weight of plants (in grams)
	Absorbed	Transpired	Retained	
1. Distilled water	6.75	6.50	0.25	
	6.55	6.20	0.35	0.60
2. $n/800$ glycocoll	6.00	5.30	0.70	
	5.05	4.50	0.55	1.40
3. $n/1,600$ glycocoll	6.15	5.90	0.25	
	4.65	4.20	0.45	0.80
4. $n/3,200$ glycocoll	7.80	7.00	0.80	
	5.28	5.20	0.08	0.95
5. $n/6,400$ glycocoll	10.25	9.50	0.75	
	8.55	8.20	−0.15	0.85
6. $n/12,800$ glycocoll	12.30	11.90	0.40	
	7.00	7.10	−0.10	0.40

Rhizomes in solutions 2–6 produced normal roots and roothairs. Best growth of roots in $n/6,400$ solution.
Atmometer, 443 cc. Temperature, 8°–31° C. Rel. humidity, 43%–100%.
Barometer, 28.85–29.95 cm.

TABLE II

TRANSPIRATION AND GROWTH OF *Scheuchzeria palustris* in HCl SOLUTIONS
November 23, to December 17, 1913

Culture solution	Amount of water in grams			Gain or loss in weight of plants (in grams)
	Absorbed	Transpired	Retained	
1. Bog water	4.00	3.60	0.40	0.40+
2. $n/400$ HCl	9.75	9.25	0.50	0.50
3. $n/800$ HCl	7.05	6.40	0.65	0.65
4. $n/1,600$ HCl	8.05	7.65	0.40	0.40
5. $n/3,200$ HCl	4.45	3.95	0.50	0.50
6. $n/6,400$ HCl	3.65	3.20	0.45	0.45
7. $n/12,800$ HCl	5.70	5.20	0.50	0.50

Plants in bog water with roots and long roothairs. Growth of roots retarded in strong acid solutions. Roots brownish and slightly gelatinized in weaker acid solutions; roothairs occasional. Atmospheric conditions as in Table VIII.

4. The insufficiency of a salt operates as a limiting factor to growth but transpiration does not decrease consistently with the retardation in growth.

5. The amount of water retained by plants is decreased when the strength of the solution is increased beyond a certain optimum concentration. The available water rather than the solute is then the

Table III

Transpiration and Growth of *Eriophorum virginicum* in Glycocoll Solutions
December 17, 1913, to January 17, 1914

Culture solution	Amount of water in grams			Gain or loss in weight of plants (in grams)
	Absorbed	Transpired	Retained	
1. Distilled water	7.00	6.80	0.20	
	8.50	8.10	0.40	0.60
2. n/800 glycocoll	10.10	9.30	0.80	
	11.60	11.30	0.30	1.30
3. n/1,600 glycocoll	10.55	9.80	0.75	
	19.55	18.40	1.15	1.98
4. n/3,200 glycocoll	11.85	11.50	0.35	
	14.55	13.90	0.65	1.20
5. n/6,400 glycocoll	11.80	11.00	0.80	
	15.20	14.10	1.10	1.95
6. n/12,800 glycocoll	9.60	8.80	0.80	
	25.40	24.70	0.70	1.65

New roots with roothairs near upper portion of rhizome, increasing in number in dilute solutions. Atmospheric conditions as in Table I.

Table IV

Transpiration and Growth of *Eriophorum virginicum* in HCl Solutions
November 23 to December 17, 1913

Culture solution	Amount of water in grams			Gain or loss in weight of plants in grams)
	Absorbed	Transpired	Retained	
1. Bog water	4.05	3.70	0.35	0.35+
2. n/400 HCl	3.70	3.70	0.00	0.00
3. n/800 HCl	3.85	3.85	0.00	0.00
4. n/1,600 HCl	3.95	3.95	0.00	0.00
5. n/3,200 HCl	4.40	4.10	0.30	0.30
6. n/12,800 HCl	3.00	2.60	0.40	0.40

Plants with new roots and roothairs in bog water solutions, and in weak acids. Root growth absent in strong solutions. Absorbing surface beginning to increase in solution No. 4. Atmospheric conditions as in Table VIII.

limiting factor. Unlike plants react differently to physiologically limiting water conditions. The variations are inherent,—peculiarities of the growth capacity and the metabolism of plants.

6. Plants may show a loss in weight but not a corresponding loss in the amount of water transpired; on the other hand, increase in growth may take place with little or no change in transpiration.

7. Changes in body weight, if taken as the measure of growth, may be pronouncedly altered by the retention of water as well as by the deposition or removal of reserve materials in the tissues. The

TABLE V

TRANSPIRATION AND GROWTH OF *Vaccinium oxycoccus* IN GLYCOCOLL SOLUTIONS
December 17, 1913, to January 17, 1914

Culture solution	Amount of water in grams			Gain or loss in weight of plants (in grams)
	Absorbed	Transpired	Retained	
1. Distilled water	4.95	4.35	0.60	
	4.35	4.30	0.05	0.65
2. *n*/800 glycocoll	9.30	8.70	0.60	
	7.85	7.70	0.15	0.75+
3. *n*/3,200 glycocoll	7.25	7.05	0.20	
	9.80	9.20	0.60	0.80+
4. *n*/6,400 glycocoll	7.65	7.10	0.55	
	7.85	7.80	0.05	0.60+
5. *n*/12,800 glycocoll	5.30	4.90	0.40	
	6.30	6.30	0.00	0.40+

New roots with mycorrhiza and devoid of roothairs; short, dense clusters in weaker solutions. Root growth best in solution No. 5. Atmospheric conditions as in Table I.

TABLE VI

TRANSPIRATION AND GROWTH OF *Vaccinium oxycoccus* IN HCl SOLUTIONS
November 23 to December 17, 1913

Culture solution	Amount of water in grams			Gain or loss in weight of plants (in grams)
	Absorbed	Transpired	Retained	
1. Bog water	3.45	3.10	0.35	0.35
2. *n*/400 HCl	6.15	5.95	0.20	0.20
3. *n*/3,200 HCl	6.20	6.00	0.20	0.20
4. *n*/6,400 HCl	5.10	4.85	0.25	0.25
5. *n*/12,800 HCl	4.85	4.45	0.40	0.40

Plants in bog water with long, thin roots, devoid of roothairs. Root growth retarded in strong acid solutions; in weaker solutions the rootcap consists of loose tissue, as if gelatinized. Atmospheric conditions as in Table VIII.

decrease in weight increment may arise through faulty nutrition and enforce compensating processes.

8. Weaker acid solutions are more effective in increasing the hydration capacity of tissues than stronger concentrations of acids, and thus are more efficient in increasing (stimulating) transpiration but not the growth of plants. The variations cannot always be attributed to differences in the absorptive surface of the root system. But whether the variations in the amount of water absorbed and held by tissues are essentially an expression of their colloidal state, or of ion concentration (osmotic pressure), or connected with hydrolytic reactions and hence with metabolism, needs further inquiry.

9. The amount of water *retained* within the plant and involved in metabolism and in the growth increment should be known as the *physiological* water requirement, to distinguish it from the other term used on the basis of the environmental water relation of the plant.

TABLE VII

TRANSPIRATION AND GROWTH OF *Coleus* sp. IN GLYCOCOLL SOLUTIONS
December 17, 1913, to March 1, 1914

Culture solution	Amount of water in grams			Gain or loss in weight of plants (in grams)
	Absorbed	Transpired	Retained	
1. Distilled water	14.70	13.65	1.15	
	21.50	21.10	0.40	1.95
	25.50	25.20	0.30	
	45.00	46.60	−1.60	−1.60
2. *n*/800 glycocoll	7.20	7.00	0.20	
	10.00	9.80	0.20	1.13
	23.70	23.20	0.50	
	34.20	35.10	−0.90	−0.90
3. *n*/1,600 glycocoll	9.80	9.80	0.00	
	22.60	21.90	0.70	0.85
	27.40	27.40	0.00	
	32.40	33.00	−0.60	−0.60
4. *n*/3,200 glycocoll	30.60	30.10	0.50	
	15.60	15.10	0.50	1.52
	23.60	23.20	0.40	
	23.00	24.70	−1.70	−1.70
5. *n*/6,400 glycocoll	50.80	49.60	1.20	2.72
	25.20	24.50	0.70	
	52.30	53.00	−0.70	−2.00
	30.30	31.50	−1.30	

Immersed portions of stem show strong curvature. Root growth best in solution No. 3. Leaves reduced in size in strong solutions; vary in form in the weaker solutions. Atmospheric conditions up to January 17, as in Table I.

The numerical relation between the quantity of water retained and the amount of growth, *i. e.*, the difference between the initial and final green or dry weight of the plant, may well be termed the coefficient of growth. This value may serve as a criterion for problems in dynamic ecology and in agriculture.

10. The retention of water is the physiological function correlated with and indispensable to growth in general, and to survival and greater areal distribution of the plants entering physically or physiologically arid habitats.

TABLE VIII.

TRANSPIRATION AND GROWTH OF *Coleus* sp. IN HCl SOLUTIONS
November 23 to December 2, 1913

Culture solution	Amount of water in grams			Gain or loss in weight of plants (in grams)
	Absorbed	Transpired	Retained	
1. Bog water	4.18	3.95	0.23	0.23
2. $n/400$ HCl	6.55	6.15	0.40	0.40
3. $n/800$ HCl	29.65	29.10	0.55	0.55
4. $n/1,600$ HCl	14.15	13.50	0.65	0.65
5. $n/3,200$ HCl	5.85	5.55	0.30	0.30
6. $n/12,800$ HCl	4.15	3.85	0.30	0.30

Color of leaves dark green in bog water, lessening in intensity as solutions decrease in concentration. Immersed portion of stem curved in stronger acid solutions and without roots; more or less gelatinized and brown. Roots and roothairs in weaker solutions; with brownish tips. Atmometer, 76.5 cc. Temperature, 8°–28° C. Relative humidity, 40%–98%. Barometer, 29.4–29.9 cm.

TABLE IX

TRANSPIRATION AND GROWTH OF WHEAT SEEDLINGS (*Triticum vulgare*) IN GLYCOCOLL SOLUTIONS

October 28 to November 5, 1913

Culture solution in duplicate series	Transpiration in grams	Green weight of plants	Dry weight of plants
1. Distilled water	81.67	5.030	0.485
2. $n/800$ glycocoll	62.40	4.935	0.580
3. $n/1,600$ glycocoll	60.05	4.480	0.515
4. $n/3,200$ glycocoll	73.10	4.980	0.535
5. $n/6,400$ glycocoll	82.75	5.415	0.515
6. $n/12,800$ glycocoll	85.10	6.655	0.535

Atmometer, 143 cc. Temperature, 15°–37° C. Relative humidity, 40%–83%.

Various other phases of the rôle of retained water—features which must enter into a conception of growth embodying the interplay and correlation of organic parts, their time relation, their changes in form and size, and their metabolism of materials and energy—have been considered briefly in another paper (8). The amount of water retained in cells and tissues determines which way biochemical reactions shall go, and it therefore becomes possible to apply this method directly to reactions which involve normal activtiy, such as respiration, pigmentation, growth curvatures, etc., as well as pathological conditions leading to death.

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